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Coarse woody debris in mixed-conifer forests, Sequoia National Park, California

MARK E. HARMON AND KERMIT CROMACK, JR.
Department of Forest Science, Oregon State University, Corvallis, OR, U.S.A. 97331
AND
BRADLEY G. SMITH
Department of Botany and Pathology, Oregon State University, Corvallis, OR, U.S.A. 97331

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The decay rate of *Abies concolor* (Gord. & Glend.) Lindl. logs and cover, mass, and volume of logs and snags in six midelevational forest stands of Sequoia National Park, California, are reported. Based on a chronosequence, *Abies concolor* boles have a decay rate-constant of 0.05 year^{-1} and a half-life of 14 years. A decay classification system was developed for *Abies concolor*, *Calocedrus decurrens* (Torr.) Florin, *Pinus jeffreyi* Grev. & Balf., and *Pinus lambertiana* Dougl. logs. Dimensions taken from maps of six permanent plots were combined with decay-class information to estimate volume, mass, and projected cover of logs and snags. Total mass ranged from 29 Mg ha^{-1} in a *Pinus jeffreyi* forest to 400 Mg ha^{-1} in a *Sequoiadendron giganteum* (Lindl.) Buchh. dominated stand. Volume, projected cover, and nitrogen storage exhibited patterns similar to mass, ranging from 84 to 1160 m^3 ha^{-1}, 3.1 to 9.3%, and 41 to 449 kg ha^{-1}, respectively.

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Le taux de carie des troncs d'*Abies concolor* (Gord. & Glend.) Lindl., de même que la couverture, la masse et le volume des troncs et des chicots dans six peuplements forestiers de moyenne altitude du Parc national Sequoia en Californie sont rapportés. D'après une chronoséquence, les troncs d'*Abies concolor* ont un taux de carie constant de 0,05 année^{-1} et une demi-vie de 14 ans. Une méthode de classement de la carie a été élaborée pour les troncs d'*Abies concolor*, de *Calocedrus decurrens* (Torr.) Florin, de *Pinus jeffreyi* Grev. & Balf. et de *Pinus lambertiana* Dougl. Les dimensions mesurées sur des cartes de six places permanentes ont été associées aux renseignements sur les classes de carie en vue d'estimer le volume, la masse et la couverture projetée des troncs et des chicots. La masse totale a varié de 29 Mg ha^{-1} dans un peuplement de *Pinus jeffreyi* à 400 Mg ha^{-1} dans un peuplement dominé par *Sequoiadendron giganteum* (Lindl.) Buchh. Le volume, la couverture projetée et l'accumulation d'azote ont montré une tendance semblable à la masse, variant de 84 à 1160 m^3 ha^{-1}, de 3.1 à 9.3% et de 41 à 449 kg ha^{-1} respectivement.

[Traduit par la revue]

Introduction

Coarse woody debris (CWD) is an important structural and functional component of temperate ecosystems (Harmon et al. 1986). A large fraction of forest production is stored as bole wood and bark, which, in unmanaged forests, eventually enters the detrital food web as CWD. In addition to serving as habitat and nutrition for many heterotrophs (Elton 1966; Käärik 1974; Swift 1977; Maser *et al.* 1978; McClelland *et al.* 1979; Frankland *et al.* 1982), CWD may also serve as autotroph habitat (Harmon *et al.* 1986). CWD strongly influences geomorphic processes on land and especially in streams and rivers (Swanson and Lienkaemper 1978; Keller and Swanson 1979) by affecting channel structure and sediment storage. The importance of logs and other woody debris in retaining finer detritus within stream reaches until it can be processed by invertebrates has recently been demonstrated (Bilby and Likens 1980). In forests, CWD accounts for 17–64% of the organic matter and 3–16% of the nitrogen returned to forest floors (Gosz *et al.* 1972; Grier and Logan 1977; Sollins *et al.* 1980). Nitrogen fixation in CWD represents a net input to the ecosystem of this important element (Cornaby and Waide 1973; Sharp and Milbank 1973; Jurgensen *et al.* 1984).

Despite its functional importance, the quantity and dynamics of CWD have been described in few studies (Harris *et al.* 1973; Grier 1978; Gosz 1980; Lambert *et al.* 1980; Tritton 1980; MacMillan 1981; Foster and Lang 1982; Graham and Cromack 1982). This lack of quantitative data limits our basic understanding of the factors controlling decay processes (Harmon *et al.* 1986). Moreover, information on CWD from relatively natural ecosystems will help assess the impact of intensive forestry practices, such as short rotations and yarding unmerchantable volume, have on this resource. CWD has not been studied previously in Sierra Nevada forests; our objective was to provide basic data on CWD quantities and dynamics. The presence of the extremely large and decay resistant species *Sequoiadendron giganteum* (Lindl.) Buchh. suggested that CWD mass in these stands could potentially reach a maximum for temperate forests. In this study, we developed (*i*) a decay classification system for logs; (*ii*) quantified the mass, nitrogen storage, volume, and projected cover of logs and snags in midelevational forests of Sequoia National Park, California; and (*iii*) determined decay rates of *Abies concolor* (Gord. & Glend.) Lindl. logs, the dominant tree species at this elevation.

Study area

The study was conducted within Sequoia National Park during 1982 and 1983. Elevations of the areas sampled ranged from 2000 to 2500 m. The climate is characterized by warm, dry summers and cool, wet winters. Mean annual precipitation is 113 cm (Rundel 1972). Mean minimum temperatures range from −6.7°C in February to 11.8°C in August, and mean maximum temperatures range from 3.4°C in December and January to 27.4°C in August (Parsons and DeBenedetti 1979). The vegetation is part of the Sierran mixed-conifer forest (Rundel *et al.* 1977), which ranges from *A. concolor* dominated stands on mesic sites to *Pinus ponderosa* Dougl. ex Laws. and *P. jeffreyi*

Grev. & Balf. dominated stands on xeric sites (Vankat 1982). In the study area, *S. giganteum* commonly occurs with *A. concolor* near meadows and streams (Rundel 1971).

Snags and logs were sampled in or near six permanent plots chosen to represent the spectrum of forest conditions within the Sierran mixed-conifer forest. National Park records indicate that fires had not occurred in these stands for >50 years. One stand, dominated by *P. jeffreyi*, on an extremely dry, rocky site near Clover Creek, was called the Jeffrey Pine Plot. Three stands dominated by *A. concolor* were sampled at Suwanee Creek. The driest was called the Sugar Pine Plot and was dominated by a mixture of *A. concolor*, *Pinus lambertiana* Dougl., *Calocedrus decurrens* (Torr.) Florin, and *P. ponderosa*. A Riparian Mixed-conifer Plot, which straddled Suwanee Creek, was established adjacent to the Sugar Pine Plot. This plot was also dominated by *A. concolor* and *P. lambertiana*, although the latter species was much less important there than in the upland plot. The third plot at Suwanee Creek had the densest canopy and was dominated by *A. concolor* and *A. magnifica* A. Murr. and was called the White Fir Plot. Two plots, called the Upper and Riparian Giant Sequoia Plots, were established in groves of *S. giganteum* at Crescent Creek. In both stands, *S. giganteum* was the dominant species in terms of biomass, although *A. concolor* had the highest densities (G. Riegel, personal communication).

Methods

Decay of Abies concolor

Twenty-five windthrown *A. concolor* logs >20 cm diameter at the large end, representing a range of conditions from fresh to extremely decayed, were sampled in the area surrounding the Crescent Creek and Suwanee Creek permanent plots. This species was selected because it was the most abundant species and appeared to decay rapidly. Residence time of logs on the forest floor was estimated by aging scars formed on adjacent trees when the log fell or "living-stumps" formed when the bole broke. Total length and end diameters were measured on each log and used to calculate log volume. In the case of extremely decayed logs with elliptical cross sections, horizontal and vertical diameters were measured. The presence or absence of needles, twigs, and branches was noted and bark cover estimated. The dimensions of pieces removed by bears were measured.

Two procedures were used to sample log density, depending upon the degree of decay. For well-decayed logs that would disintegrate with chainsaw cutting (i.e , >35 years old), two to five samples were taken using a 51 mm diameter corer. For logs <35 years old, four to five cross sections 5 to 10 cm thick were removed with a chainsaw. Zones of sapwood and heartwood, both rotten and sound, as well as insect galleries were mapped in the field onto clear plastic, and then area was computed in the laboratory with an electronic digitizer. A sample was taken from each mapped zone with 51 mm diameter corer for well-decayed wood and a chisel for sound wood. Exterior dimensions were measured in the laboratory, and volume was calculated for the appropriate geometric solid. All samples were dried at 55°C for 96 h and weighed.

For logs <35 years old cross-sectional density was calculated by weighting sample density by proportional area. Log wood density was estimated by weighting cross-sectional density by area. For logs >35 years old, log density was calculated as the unweighted mean of sample densities. Decreases in density underestimated the fraction of mass lost when fragmentation removed volume from well decayed logs. In order to include fragmentation losses, the initial volume of fragmented logs was estimated using the regression equation based on logs <10 years old:

$$[1] \quad Y = 0.00003\,X^{2.81}, \qquad r^2 = 0.989, N = 17$$

where Y is the bole volume (m^3) and X is the diameter at breast height (dbh) along the bole (cm). Since all logs >35 years old were aged using living stumps, the original dbh could be measured. The fraction of bole volume remaining was then multiplied by log density to give an index of the original mass remaining. Since the original density was unknown, this index is represented as a density and not a proportion.

The fraction of original primary branches remaining on each log was estimated by dividing current number by the original number. The latter was estimated by counting branch whorls on the bole and multiplying by the mean number of primary branches per whorl (~5) from live trees. Branchwood decay for logs <7 years old was estimated from density changes. Ten primary branches of each log were sampled by removing a 10 to 20-cm long cylinder with a handsaw. The external dimensions of these branch samples and oven-dried weights were used to determine density.

Bark decay rates were determined from density changes for logs <20 years old. A subsample of bark was removed from each cross section. In the laboratory, outer bark was separated from the inner bark after the samples had been cut to form cylinders or rectangular solids. Exterior measurements were used to estimate volume, and dry weight was determined after oven drying for 96 h at 55°C.

To test the effect of diameter on decay, cross-section densities adjusted for volume loss were log-transformed and used in a stepwise regression analysis. The decline in density of wood, bark, and branch density was modeled as a negative exponential function of time using the equation

$$[2] \quad D_t = D_0 e^{-k_d t}$$

where D_t is density (g cm^{-3}) at time t (years), D_0 is the initial density (g cm^{-3}), and k_d is the decay rate constant for density. Preliminary analysis indicated sapwood and heartwood decayed at similar rates; therefore their density was averaged for this analysis. To calculate initial density and decay rate constant, densities were transformed to natural logarithms and least-squares linear regression was used. Changes in bark cover and fraction of branches remaining were modeled using the following function:

$$[3] \quad V_t = 1 - (1 - e^{-k_f t})^N$$

where V_t is the proportion of volume left at time t (years), k_f is a fragmentation rate constant, and N is a dimensionless parameter that induces a lag time in the decay curve. This function was preferred over the simple negative exponential curve because both bark and branches did not begin to fall off until a lag time had been exceeded. Nonlinear regression methods (SAS Institute 1979) were used to estimate these parameters. All statistical tests were judged significant if $0.01 < p < 0.05$ and highly significant if $p < 0.01$.

Log decay classes

It was impractical to sample each log in the plots for density to calculate CWD mass. An alternative approach was to define decay classes and sample these for density and nitrogen content. To establish log decay classes, a set of unaged logs of *A. concolor*, *C. decurrens*, *P. jeffreyi*, and *P. lambertiana* was examined for external, visual characteristics that correlated to the degree of decay. *Sequoiadendron giganteum* was not sampled because of its extremely large size and value as a natural resource in the park. External characteristics that were recorded included the presence of needles, twigs, branches, bark on branches, case hardening, lichens, mosses, fungal fruiting bodies, carpenter ants, and termites. Bark cover, cross-sectional shape, and whether the sapwood and (or) heartwood was friable (i.e., could be crushed by hand) were also noted. Sampling of these logs for wood density was similar to that of aged *A. concolor* logs except that two samples or cross sections were removed 1 m in from the ends.

In the case of *A. concolor* and *P. jeffreyi*, reciprocal averaging (Hill 1973) was used to ordinate logs on a continuum using the presence or absence of traits. Reciprocal averaging (RA) is a multivariate eigenvector method that orders both sample units (in this case logs) and characteristics along axes. Those logs or characteristics most similar appear close together along the axes.

Four log decay classes, based on easily observed external characteristics that exhibited a high degree of constancy, were subjectively chosen for each species. Mean wood density, volume of insect excavations, and bark cover were calculated for each decay class within species.

Log and snag mass

Mass of logs and snags >15 cm in diameter and >1.5 m long was determined in each of the six forest plots. The product of volume and density was used to estimate the mass of each decay class. Volume was calculated from length and end diameters of pieces. Snag upper diameter was estimated assuming a taper of 2 cm m^{-1}, which was the average taper observed for logs. In the case of logs with elliptical cross sections, vertical and horizontal diameters were measured. Snag height was estimated visually after heights of several snags in each plot had been measured with a clinometer.

The densities of snag and log decay classes were assumed equal. *Sequoiadendron* did not appear decayed and therefore its density was assumed to be equivalent to fresh, green, clear wood (0.39 g cm^{-3}, U.S. Forest Products Laboratory 1976). *Abies magnifica* wood density was assumed to be equivalent to that of *A. concolor* for all decay classes.

Nitrogen and carbon analysis

Wood density samples of each species and decay class were ground in a Wiley mill to pass through a 40-mesh screen. Prior to analysis for N and C content, samples of sapwood and heartwood in decayed and undecayed condition were composited in proportion to their volume in a log. N content was determined by micro-Kjeldahl digestion (selenium – copper sulfate – potassium sulfate catalyst) followed by measurement of ammonium with an autoanalyzer (Technicon method 33-4-24-A/A), and C content was determined using a Leco 12 automatic analyzer. Mean N and C content and C:N ratios were calculated for each species and decay class sampled. Total N storage was calculated by multiplying the mass of each decay class and species by its mean N concentration. Since *S. giganteum* could not be sampled, we assumed the N content was 0.1%, which was equal to the mean of the sampled species. *Abies magnifica* N concentrations were assumed to be equal to that of *A. concolor*.

Results and discussion

Abies concolor *decay rates*

Abies concolor boles decayed very rapidly and had almost disappeared in 60 years (Fig. 1). The regression equation of bole density adjusted for volume losses versus time was highly significant:

$$[4] \quad D_t = 0.396e^{-0.049t}, \qquad r^2 = 0.83,\ N = 25$$

The equation indicated 50% of an *A. concolor* bole would remain in 14 years and that 95% would disappear in 61 years. The estimated initial wood density is quite similar to the 0.41 g cm^{-3} measured for undecayed wood.

Boles must decay for at least 24 years before volume decreases to a measurable extent (Fig. 2). Upper portions of boles disappeared faster than basal portions. However, stepwise regression analysis did not indicate that cross-section diameter or its interaction with time had significant effects on wood density. In contrast, time had a highly significant negative correlation with density.

Many years were required before boles were fully colonized by decomposers. Advanced decay progressed into *A. concolor* boles at a mean rate of 1 cm $year^{-1}$. Multiple regression analysis using log age and cross-section diameter as independent variables indicated a small and barely significant effect of diameter on the depth of decay. Large-diameter cross sections were penetrated slower than small ones. This suggests that larger diameter logs would take longer to be colonized and would therefore decay slower than smaller ones.

Wood volume excavated by insects increased with log age. The Spearman rank correlation between time and volume excavated was highly significant ($r_s = 0.67$, $N = 20$). Logs <6 years old were rarely attacked by carpenter ants (*Camponotus* spp.) or termites (*Zootermopsis nevadensis* Hagen) and after this time, insects excavate wood volume at a rate of ~0.70% $year^{-1}$.

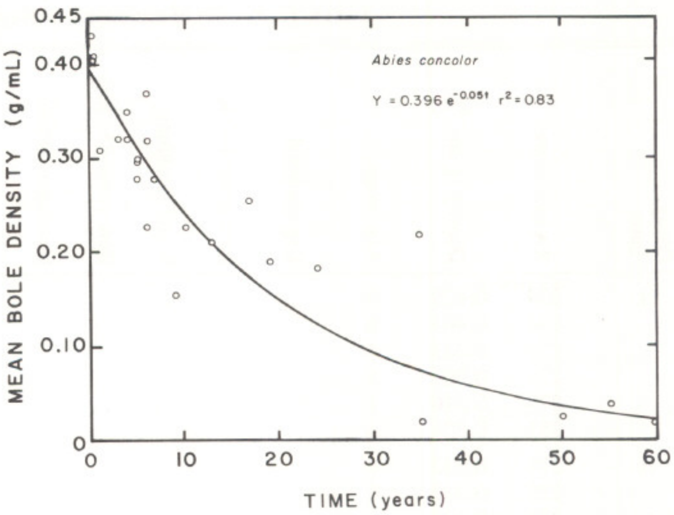

FIG. 1. Mean density of *Abies concolor* boles as a function of time since falling. The density of boles on the ground for more than 24 years was adjusted to reflect volume losses.

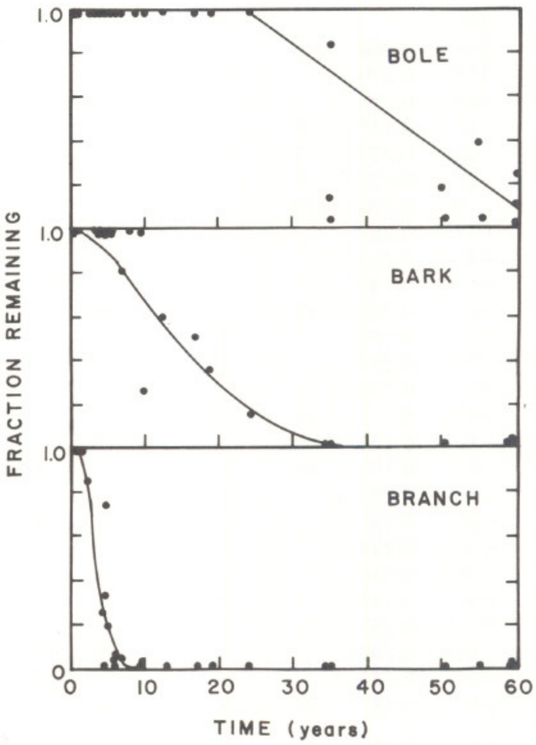

FIG. 2. Fragmentation of *Abies concolor* boles, bark, and branches.

Bole wood of *A. concolor* appears to decay faster than that of other conifers which have been studied using chronosequences. The degree this difference is attributable to climate, size, or substrate quality is difficult to discern. In New Hampshire, *Abies balsamea* has a decay rate constant of 0.03 $year^{-1}$ (Lambert *et al*. 1980). While the substrate quality of these two *Abies* is probably fairly similar, *A. balsamea* logs were smaller and presumably decayed in a cooler climate than *A. concolor* logs. Assuming decay rate decreases with size, this would indicate decay rate increases with temperature. *Pseudotsuga menziesii* and *Tsuga heterophylla* logs of similar size to *A. concolor* have been studied in Oregon (Grier 1978; Graham 1982). Neither *Abies* nor *Tsuga* are considered decay resistant (U.S. Forest Products Laboratory 1967) and their lignin content is similar (Harmon *et al*. 1986). Therefore differences in decay

TABLE 1. Results of reciprocal averaging analysis (RA) of *Abies concolor* logs

Decay class	RA axis score	Density (g cm^{-3})	Age (years)	Log scattered	Bark cover 0–5%	Wood sloughing	Bark cover 25–50%	Heartwood friable	Log collapsing	Sapwood friable	Bark cover 5–25%	Bark cover 75–95%	Ants and termites	Bark loose	Bark cover 50–75%	Bark on branches	Branches	Bark cover 95–100%	Lichens	Twigs	Needles
I	334	0.429	0													+	+	+	+	+	+
	334	0.407	0													+	+	+	+	+	+
	279	0.323	4											+		+	+	+		+	+
	279	0.301	5											+		+	+	+		+	+
	279	0.310	1											+		+	+	+		+	+
	253	0.301	5											+		+	+	+		+	
II	225	0.352	4											+		+	+	+			
	225	0.317	6											+		+	+	+			
	225	0.190												+		+	+	+			
	223	0.372	6											+				+	+		
	216	0.323	3											+		+	+	+	+	+	
	173	0.260					+		+					+		+	+	+	+	+	
	168	0.475												+				+			
III	168												+	+				+			
	163	0.284	5										+	+		+	+	+			
	153	0.220					+		+				+	+		+		+			
	144	0.398						+						+	+	+	+			+	
	62	0.155	9					+	+				+	+				+	+		
	26	0.277	7									+		+		+	+				
	23	0.227	6						+	+			+	+		+	+				
	8	0.226	10		+				+				+	+	+		+				
	−38	0.287			+	+	+				+		+	+		+					
	−44	0.226									+			+							
	−67	0.146									+	+	+	+							
	−69	0.255	17			+		+	+	+			+	+	+						
	−75	0.276			+								+	+							
	−77	0.256						+		+	+		+	+							
	−77	0.278						+		+	+		+	+							
	−82	0.211	13					+	+	+		+	+	+							
	−85	0.122				+		+		+	+		+	+							
	−87	0.191	19				+	+	+	+			+	+							
	−88	0.240				+		+	+	+		+	+	+							
	−89	0.151				+	+	+		+			+	+							
	−92	0.194		+					+	+	+	+	+	+							
	−92	0.210			+	+				+				+							
	−93	0.140		+				+	+	+	+		+	+							
	−94	0.255			+	+		+		+			+	+							
	−94	0.209			+	+		+		+			+	+							
	−96	0.150		+			+	+	+	+			+	+							
	−97	0.182	24	+		+		+	+	+	+		+	+							
IV	−97	0.196	35		+	+		+	+	+			+	+							
	−97	0.201		+	+		+	+	+			+	+								
	−100	0.266		+	+			+	+	+			+	+							
	−100	0.140		+	+			+	+	+			+	+							
	−100	0.168		+	+			+	+	+			+	+							
	−100	0.198		+	+			+	+	+			+	+							
	−100	0.222		+	+			+	+	+			+	+							
	−100	0.200		+		+	+	+	+	+			+	+							
	−103	0.146	35	+	+	+		+	+	+			+	+							
	−103	0.132	50	+	+	+		+	+	+			+	+							
	−103	0.162	60	+	+	+		+	+	+			+	+							
	−103	0.172		+	+	+		+	+	+			+	+							
	−106	0.152	60	+	+	+		+	+	+			+	+							
	−106		80	+	+	+		+	+	+			+	+							
	−106	0.083	55	+	+	+		+	+	+			+	+							
	−119	0.250		+	+	+		+	+	+			+	+							

NOTE: The RA scores of logs and variables have been ordered from high to low; logs or variables with highest scores indicate the least decayed states, whereas those with the lowest scores indicate the most decayed states. The presence of a variable for a log is indicated by a + . Wood density and age of logs are also indicated.

rate should be due to climatic factors. Decay rate decreases from 0.05 year^{-1} for *A. concolor* in Sequoia to 0.02 year^{-1} for *T. heterophylla* in the Oregon Cascades (Graham 1982) to 0.01 year^{-1} for *T. heterophylla* on the Oregon coast (Grier 1978). Mean annual temperature is ~10°C at all three sites, but precipitation increases from 113 cm in Sequoia to 250 cm in the Cascade Range to 342 cm in the Oregon coast. This indicates a negative correlation between decay rate and precipitation, at least for the range examined. *Pseudotsuga menziesii* probably decays slower than *A. concolor* because of increased precipitation, and greater decay resistance of the former species heartwood.

The density decay equation for branches <7 years old was highly significant:

$$[5] \quad D_t = 0.613\,e^{-0.039t}, \qquad r^2 = 0.647,\ N = 12$$

Estimated initial density was very close to that measured for undecayed branches (0.628 g cm^{-3}). The equation indicates 50% of the branchwood disappears in 18 years and that 95% disappears in 77 years. However, the decay rate constant is certainly too low because no branchwood was observed near boles >35 years old. To disappear within this time, the branch decay rate constant would have to be at least 0.09 year^{-1}. The lag time associated with branch fall was <3 years (Fig. 2). After 6–10 years, most of the branches not removed when the bole originally fell had fallen to the forest floor. Non-linear regression analysis indicated branch fall could be described by the following equation:

$$[6] \quad V_t = 1 - (1 - e^{-0.696t})^{8.053}, \qquad r^2 = 0.87,\ N = 26$$

where V_t is the proportion of branches remaining.

Outer bark of *A. concolor* logs did not decrease in density after 20 years of decay. Regression analysis indicated a nonsignificant relationship between outer bark density and time. This may have been due in part to the difficulty in measuring outer bark volume due to its irregular surface. Mean density of bark remaining on boles was 0.509 g cm^{-3} (SE = 0.023, N = 15). Inner bark density declined significantly with time, but the rate constant was lower than expected, given the relatively nutrient rich nature of this substrate (Smith and Zavarin 1960). The regression equation describing inner bark density changes over time was

$$[7] \quad D_t = 0.656\,e^{-0.027t}, \qquad r^2 = 0.387,\ N = 14$$

This equation predicts that inner bark density decreases 50% in 25 years and 95% in 109 years. Bark began to slough from *A. concolor* boles after 7–10 years, and most was gone after 35 years (Fig. 2). The nonlinear regression of bark cover as a function of time was

$$[8] \quad V_t = 1 - (1 - e^{-0.107t})^{2.57}, \qquad r^2 = 0.83,\ N = 26$$

This equation indicated that it takes 13 years for 50% of the bark to fall off and 37 years for 95% of the bark to fall off.

Unlike the wood decay curve (Fig. 1), the bole decay curve including bark does not follow an exponential pattern. From time zero until year 8, the entire bole decays slightly slower than wood, primarily because the outer bark does not decrease in density. Between years 8 and 26 the entire bole decays faster than wood because bark is rapidly fragmenting. After 26 years, the bole is relatively bark free and the overall decay curve parallels the wood decay curve, but has ~2% less mass remaining than wood alone. While the two decay curves differ, the large proportion of original mass in wood dampens out the influence of bark on the overall curve.

Reciprocal averaging analysis

Reciprocal averaging analysis ordered *A. concolor* logs along a decay continuum that corresponded to age and density changes (Table 1). There were highly significant Spearman rank correlations between the first RA axis and *A. concolor* wood density ($r_s = 0.84$, $N = 53$) and log age ($r = 0.96$, $N = 26$). The ordering of characteristics by RA (Table 1) indicated the following series of events during *A. concolor* log decay: (1) needles fall off, (2) twigs fall off, (3) branches fall off, (4) bark falls off and ants invade, (5) the sapwood becomes friable, (6) parts of the log collapse and settle to the forest floor, (7) the heartwood becomes friable, (8) pieces of wood slough off the log, and finally (9) the cross section of the entire log becomes elliptical and remaining fragments become scattered across the soil surface.

RA ordered *P. jeffreyi* logs along a decay continuum similar to that of *A. concolor* (Table 2). The Spearman rank correlation between *P. jeffreyi* wood density and the first RA axis score was not significant ($r_s = 0.463$, $N = 20$). The lack of correlation is probably because decayed wood sloughs off *P. jeffreyi* logs until they are quite old. This means density remains fairly constant in spite of decay.

Decay classes

Although grouping logs by decay classes was not as revealing as RA analysis, the basic trends in decay patterns emerged for all four species examined (Table 3). In spite of the continuous nature of the decay process, there were certain characteristics that could be used to identify classes (Table 1). For example, the presence of needles and twigs distinguished class I *A. concolor* from other classes; the lack of bark and elliptical cross-sectional shapes separated class IV *A. concolor* from other classes.

In all four species, the retention of needles, twigs, branches, and bark decreased from class I to class IV. The volume excavated by insect increased with decay class, reaching a maximum of 2–11% in class III. In class IV logs, the fragmentation and collapse of logs made gallery volume determination difficult. However, few active galleries were observed in class IV logs, so the peak in excavations probably occurred in class III logs. Density generally decreased with decay class. In *A. concolor* the change was gradual, whereas with *P. jeffreyi*, density remained fairly constant until class IV.

Carbon and nitrogen content

Carbon concentration of logs did not exhibit a consistent change with decay class and averaged 51% (Table 4). In contrast, N concentration increased from 0.09–0.11% in class I logs to 0.25–0.35% in class IV logs. C:N ratios for class I logs ranged from 457 in *P. lambertiana* to 572 in *P. jeffreyi*. As decay proceeded, the ratios narrowed so that they ranged from 114–276 for class IV logs.

Total N storage in CWD also followed overall mass patterns, with a minimum of 41 kg/ha in the Jeffrey Pine Plot and 449 kg/ha in the Riparian Giant Sequoia Plot (Table 5). Logs accounted for more stored N than snags even when snag mass exceeded that of logs. For example, snags stored 57% of the mass in the White Fir Plot, but only 47% of the N. This is caused by the greater mass of older, N-rich wood in logs.

Amounts of N stored in dead tree boles in the *A. concolor* dominated stands are comparable to those found in a chronosequence of *Pseudotsuga* dominated stands in the Cascades of Oregon and Washington (Harmon *et al.* 1986). Nitrogen storage in the Giant Sequoia Riparian Plot was estimated to be two to four times greater than these values, primarily because of the large CWD mass found there. The Jeffrey Pine Plot had

TABLE 2. Results of reciprocal averaging analysis (RA) of *Pinus jeffreyi* logs

Decay class	RA axis score	Density (g cm^{-3})	Bark cover 0–5%	Log scattered	Sapwood sloughing	Log collapsing	Sapwood friable	Heartwood friable	Ants and termites	Bark cover 5–25%	Bark loose	Bark cover 75–95%	Bark cover 50–75%	Branches	Bark on branch	Bark cover 25–50%	Twigs	Bark cover 95–100%	Needles
I	271	0.372									+			+	+		+	+	+
	271	0.268									+			+	+		+	+	+
	271	0.363									+			+	+		+	+	+
II	167	0.335							+		+			+	+	+	+		
	118	0.357							+		+		+	+	+				
	100	0.266						+	+		+	+		+					
	85	0.581							+	+	+			+	+				
	58	0.288						+	+	+	+			+	+				
	32	0.365					+	+	+	+	+			+	+				
	9	0.212				+	+	+	+	+	+			+	+				
III	−33	0.278					+		+	+	+								
	−86	0.398		+	+	+	+	+	+	+	+								
	−101	0.427	+		+	+	+	+	+		+								
	−106	0.255	+		+	+	+		+		+								
IV	−109	0.398	+	+	+	+	+	+	+		+								
	−109	0.126	+	+	+	+	+	+	+		+								
	−109	0.160	+	+	+	+	+	+	+		+								
	−109	0.159	+	+	+	+	+	+	+		+								
	−109	0.202	+	+	+	+	+	+	+		+								
	−114	0.131	+	+	+	+	+	+	+		+								
	−114	0.280	+	+	+	+	+		+		+								

NOTE: The RA scores of logs and variables have been ordered from high to low; logs or variables with highest scores indicate the least decayed states, whereas those with the lowest scores indicate the most decayed states. The presence of a variable for a log is indicated by a +. Wood density of logs is also indicated.

TABLE 3. Wood density, bark cover of boles, and volume of wood excavated by insects for each decay class of *Abies concolor*, *Lebocedrus ducurrens*, *Pinus jeffreyi*, and *Pinus lambertiana*

Decay class	Wood density (g cm^{-3})	Bark cover (%)	Insect excavations, volume (%)
	Abies concolor		
I	0.369 (0.024, 8)[a]	100 (0, 7)	0 (0,8)
II	0.305 (0.027, 7)	95 (3.3, 9)	0.14 (0.14, 8)
III	0.212 (0.010, 24)	40 (7.4, 25)	5.26 (0.93, 20)
IV	0.178 (0.013, 14)	3 (1.5, 16)	—[b]
	Calocedrus decurrens		
I	0.425 (—,[b] 1)	100 (—, 1)	0 (—, 1)
II	0.356 (0.039, 3)	96 (4.3, 3)	2.35 (1.39, 3)
III	0.331 (0.032, 4)	13 (8.7, 4)	2.25 (0.91, 4)
IV	0.156 (—, 1)	1 (—, 1)	—
	Pinus jeffreyi		
I	0.365 (0.026, 5)	100 (0, 5)	0.50 (0.49, 5)
II	0.343 (0.045, 7)	29 (12.3, 7)	9.25 (3.67, 7)
III	0.340 (0.043, 4)	1.2 (0.7, 5)	10.81 (3.00, 4)
IV	0.176 (0.023, 6)	0 (0, 6)	—
	Pinus lambertiana		
I	0.369 (0.037, 4)	100 (0, 4)	0 (0, 4)
II	0.269 (—, 1)	3 (—, 1)	18.64 (—, 1)
III	0.221 (0.023, 6)	0.7 (0.4, 7)	6.28 (2.21, 5)
IV	0.125 (0.019, 5)	0.6 (0.4, 5)	—

[a] $\bar{x}$ (SE, *N*).
[b] Could not be estimated.

TABLE 4. Concentrations of carbon and nitrogen, and C:N ratio for various species and decay classes of dead tree boles from Sequoia National Park

Decay class	N concn. (%)	C concn. (%)	C:N
	Abies concolor		
I	0.10 (0.01, 7)[a]	48.80 (0.29, 7)	488
II	0.13 (0.02, 9)	49.92 (0.66, 9)	384
III	0.17 (0.02, 7)	48.85 (0.72, 9)	287
IV	0.25 (0.01, 5)	53.37 (1.04, 6)	213
	Calocedrus decurrens		
I	0.09 (—[b], 1)	51.37 (—, 1)	571
II	0.14 (0,2)	50.96 (1.30, 2)	364
III	0.17 (0.03, 2)	51.18 (1.40, 2)	301
IV	0.25 (—, 1)	48.20 (—, 1)	193
	Pinus jeffreyi		
I	0.09 (0.01, 3)	51.45 (1.29, 3)	572
II	0.15 (0.01, 2)	50.66 (1.67, 2)	338
III	0.12 (—, 1)	50.30 (—, 1)	419
IV	0.36 (0.04, 3)	51.79 (1.35, 3)	144
	Pinus lambertiana		
I	0.11 (0.01, 2)	50.33 (0.66, 2)	457
II	0.19 (—, 1)	53.63 (—, 1)	282
III	0.22 (0.02, 2)	51.57 (2.30, 2)	234
IV	0.20 (0.05, 2)	55.20 (0.95, 2)	276

[a] $\bar{x}$ (SE, *N*).
[b] Could not be calculated.

TABLE 5. Volume, biomass, projected cover, and nitrogen content of logs and snags for the six reference stands established in Sequoia National Park

Plot	Volume (m^3/ha)		Biomass (Mg/ha)		Projected cover (%)		Nitrogen (kg/ha)	
	Snags	Logs	Snags	Logs	Snags	Logs	Snags	Logs
Upper giant sequoia (2.5 ha)[a]	80.9	340.0	27.4	110.7	1.27	5.64	32.2	134.7
Riparian giant sequoia (2.0 ha)	55.9	1104.5	16.6	383.0	0.86	8.39	22.3	426.5
Sugar pine (1.12 ha)	130.4	151.0	42.9	32.6	1.92	4.51	54.1	61.5
White fir (0.87 ha)	178.3	151.0	51.9	48.7	2.82	6.82	73.1	86.0
Riparian mixed conifer (1.31 ha)	68.2	242.9	22.5	67.1	1.05	5.93	28.5	98.6
Jeffrey pine (1.0 ha)	2.0	82.5	0.7	28.0	0.04	2.08	1.1	40.0

[a] Permanent plot size.

relatively little N storage compared with other conifer ecosystems. Nevertheless, N storage here was still four times the 9-11 kg ha^{-1} reported for two deciduous forests (Duvigneaud and Denaeyer-DeSmet 1970; Henderson *et al.* 1978).

Log and snag mass

Coarse woody debris (CWD) mass ranged from a low of 29 Mg/ha in the Jeffrey Pine Plot to a high of 400 Mg/ha in the Riparian Giant Sequoia Plot (Table 5). The three *A. concolor* dominated stands (i.e., Sugar Pine, Riparian Mixed-conifer, and White Fir) had CWD mass of 75–101 Mg/ha. The Upper Giant Sequoia Plot had a CWD mass only slightly larger than the *A. concolor* dominated stands. The extremely high mass of the Riparian Giant Sequoia Plot was primarily due to an abundance of *S. giganteum* logs. Excluding this species, CWD mass in this stand was 52 Mg/ha. The proportion of mass as snags also varied widely among the stands. Snags formed only 2.4% of the mass in the Jeffrey Pine Plot. In contrast, the *A. concolor* dominated plots had 25–57% of their CWD mass as snags. In spite of the large amount of CWD mass, projected cover was <10% for all stands (Table 5). CWD volume exhibited the same pattern as mass with a minimum of 84.5 m^3 ha^{-1} in the Jeffrey Pine Plot and a maximum of 1160.4 m^3 ha^{-1} in the Riparian Giant Sequoia Plot (Table 5).

The amount of CWD found in mixed-conifer forests encompasses the range observed for undisturbed, temperate coniferous forests (Harmon *et al.* 1986). The extremely large size and decay resistance of trees in the giant sequoia plots leads to the highest accumulation of CWD reported yet for undisturbed forests. In contrast, the Jeffrey Pine Plot was lower than most conifer forests, with the exception of *Pinus contorta* in Wyoming (Fahey 1983). Low productivity and tree biomass in *P. jeffreyi* stands may reduce CWD input rates and thus mass. On the other hand, *P. jefferyi* boles contain more sapwood than other conifer species in the region (Kimmey 1955) and this may lead to faster decay and reduce CWD accumulations.

The wide range in CWD mass in relatively undisturbed forests of Sequoia National Park reflects the variation of input and decay rates and also suggests the functional importance of this material varies dramatically among forest types. The function of CWD in the nitrogen cycling and productivity of these forests is unknown. The relative lack of nurse logs in these forests suggests plants utilize CWD only after considerable decay has occurred. The point at which this material with high C:N and lignin:N ratios releases nutrients is unknown, but crucial to understanding the role of CWD in forest nutrition (Aber and Melillo 1982; Berg 1986; McClaugherty and Berg 1987). Finally, CWD is an important invertebrate habitat in Sequoia National Park. Given the heavy predation of bears on termites and carpenter ants, CWD may be an important trophic component of these forests.

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